Seasonal Variations in Food Supply for Wild Primates

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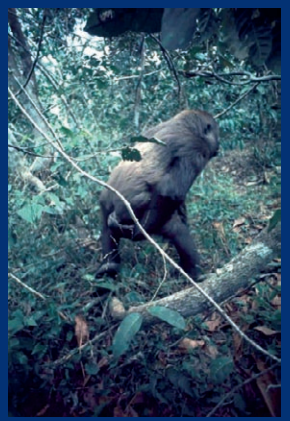
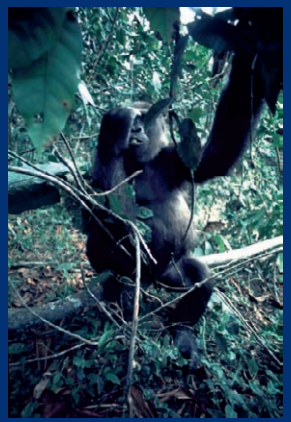
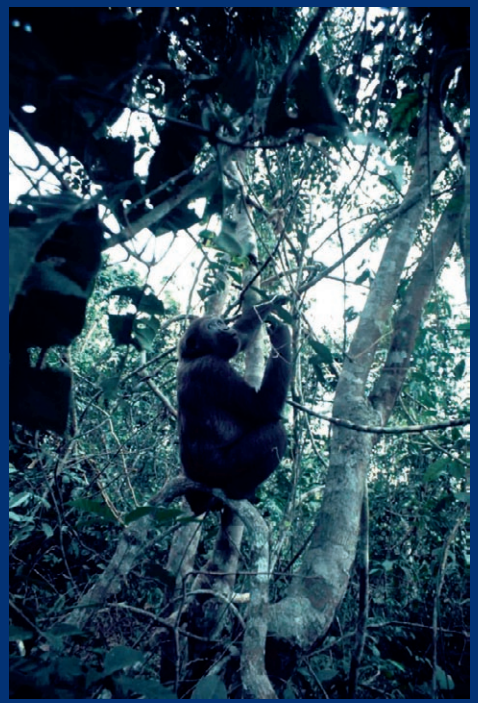
Coprophagie
Ikata, jeune gorille mâle
observé le 14 février 1975 sur un îlot de l'Ivindo







Seasonal Variations in Food Supply for Wild Primates

C. M. Hladik

During the last few decades, a primate model has been developed to understand the biological background of human behaviour, and no zoological group was studied so intensively in terms of behavioural physiology, and the significance of the different adaptive strategies in the natural environment.

To limit this rich zoological model to a small number of species (among the genera *Macaca*, *Papio*, and *Pan*), or simply to the rhesus monkey (*Macaca mulatta*), as frequently presented in biomedical papers, is an oversimplification of the different comparative aspects. On the contrary, it is important to consider the whole primate order with its numerous radiations (including about 175 species, from pure insectivorous to ruminant-like, leaf-eating forms) to reflect a general background rich enough in different elements of physiological ecology, and in which most of the supposed characters participating in human evolution can be found.

In this context, during my different field studies on wild primates, I have been particularly impressed by the importance of seasonal variations, even for species living in a supposed 'stable' environment such as the tropical rain forest. This might reflect that the annual variation in food supply, and the subsequent seasonal variations in the diet of the different species, is the common basis of primate feeding behaviour. Facing such variations has certainly been an important motor of evolution; the measure of these variations among the extant species provides a basis to understand past and present selective pressures.

THE PROSIMIAN CASE STUDY

Generally considered as a model of our remote ancestors (Charles-Dominique and Martin 1970), the extant prosimians, Lemurs, Galagos, and Lorises, present a mosaic of primitive characters that can be mixed with the most specialized adaptations. This is particularly the case of the leaf-eating forms (genera *Indri* and *Lepilemur*) in which teeth and digestive tract are almost as sophisticated as those of the Artiodactyla and Lagomorpha (Hladik 1979; Chivers and Hladik 1980).

The 'unspecialized' species, in terms of dietary adaptation, that is to say, the various forms feeding on a mixture of fruit and small invertebrate prey, are presumably close to a line that can be traced from the primitive stock to the

Anthropoids. Among different prosimians with such an unspecialized diet, my colleagues and I recently found a surprising range of seasonal variation in terms of food supply, food intake, and dietary composition (Hladik, Charles-Dominique, and Petter 1980). Two species are particularly interesting to observe: the fat-tailed dwarf lemur, *Cheirogaleus medius*, and the lesser mouse lemur, *Microcebus murinus*.

These two nocturnal prosimian species live in the forest of the west coast of Madagascar, in sympatry with other nocturnal and diurnal forms, and the aim of our study was to determine the extent of possible overlap in the diets and the different processes preventing competition for food.

Different methods were applied to measure food availability throughout the year in the natural environment, and the converging results, presented in Fig. 1.1, illustrate the importance of seasonal variations. In fact, the forest of the west coast of Madagascar is in a dry climatic zone subject to a severe dry season lasting for about six months. Accordingly, most plant species respond with an extremely precise flushing cycle influencing not only plant production, but also, to a large extent, the seasonal availability of the animal prey (Hladik 1980).

Food availability (Fig. 1.1) presents a series of annual peaks: the flowers of many tree species is the most important food resource (nectars and pollens) during the months of October and November, at the end of the dry season, and before the beginning of the rains. In December and during the rest of the rainy season, large amounts of new leaves allow a progressive increase in the

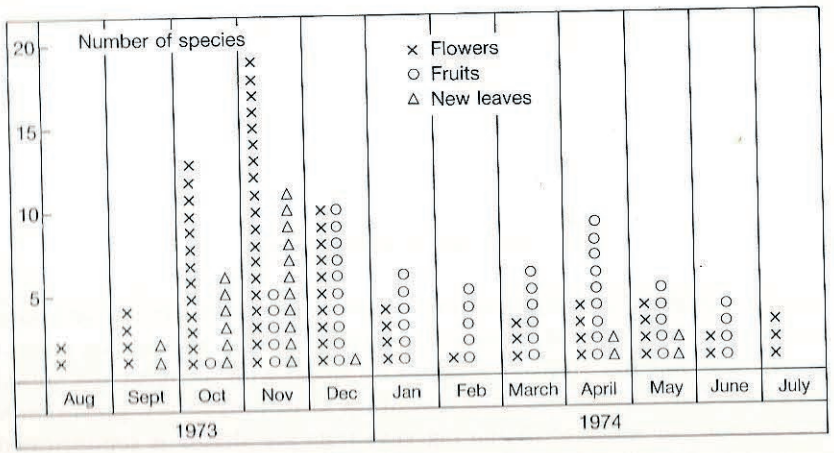


FIG. 1.1. Seasonal variation of food availability in the forest of the west coast of Madagascar, according to the number of species producing potential foods (fruits, flowers, and new leaves) in a plot of 2200 m². The flowering peak, in the October–November period, precedes the beginning of the rainy season (December–May) during which fruits and leaf flushing are abundant (after Hladik *et al.* 1980).

invertebrate fauna biomass (reaching a maximum in the April–May period after the analysis of caterpillars' faeces in the samples of litter fall). The occurrence and ripening of the fruits of different plant species also progressively increases and lasts until the beginning of the dry season (June). We can summarize this cycle of food availability as a sudden burst in the supply of carbohydrates (nectars, in October) followed by a progressive increase in the availability of animal protein (invertebrates) concommitent with a large production of fruit. During the dry season the rare food resources can be used only by specialized species previously described in Hladik *et al.* (1980).

The lesser mouse lemur and the fat-tailed dwarf lemur essentially harvest the 'surplus' food available before the beginning of the rainy season and during it. During this period, the composition of their respective diets undergoes considerable variations that imply a concomitant physiological adaptation.

The diet of the fat-tailed dwarf lemur was determined by direct observation, at night, and from the analysis of faecal material collected when the animals were caught for marking. Fruits formed the staple food (together with nectars and pollen at the beginning of the period of activity). Invertebrates were present in 50 per cent of the faeces, but in small amounts, the volume of chitin never exceeding 10 per cent of the other food remains. In general, the fat-tailed dwarf lemur appears as an opportunistic frugivore complementing its diet with the most abundant and nutritious food types.

The most characteristic feature of the fat-tailed dwarf lemur is the ability to store large quantities of fat in its tail, which can take the shape of a large sausage (thus its peculiar name, 'fat-tailed'), and the subsequent ability, after fattening, to hibernate for at least six consecutive months, and, in some instances, for up to eight months of the dry season. During this period, the animals retire inside deep holes in tree trunks where three to five individuals may be piled upon each other, separated by a kind of soft lodge made of wet decaying wood. Such a physiological response to the shortage of food resources and/or drastic change in climatic conditions is common in certain mammalian orders (Rodentia) but exceptional among the primates.

Accordingly, the annual variation of body weight observed in the wild (Fig. 1.2) is the largest among primates. Due to tail and body fattening, weight increases from 142 g (standard deviation = 12) up to 217 g (standard deviation = 26) in adults. Note the important scatter in March, perhaps due to the individual social status: one of the adult males (number 17, probably a peripheral) lost weight and certainly died before the next rainy season. After March, except for this last animal, only juveniles were caught in our traps; all the other adults were hibernating. This obviously prevents competition for food and allows the young animals to reach a maximum body weight to be able to face their first dry season.

A further analysis of the system of periodical fattening of the fat-tailed dwarf lemur has been conducted experimentally in our laboratory, at Brunoy. During the experiment, lasting for three years (Petter-Rousseaux and Hladik 1980), the

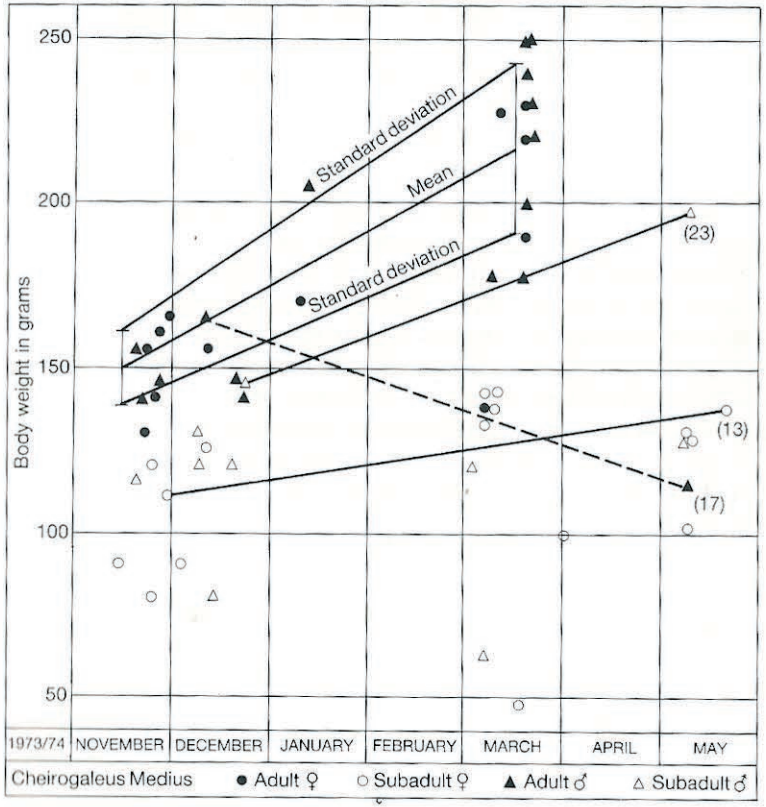


FIG. 1.2. Seasonal variation of body weight of the fat-tailed dwarf lemur, *Cheirogaleus medius*, in the forest of the west coast of Madagascar, according to the data from captured and recaptured marked wild animals (after Hladik *et al.* 1980).

animals were fed on a standard diet, and the parameters simulating field conditions included day-length, temperature, and, as far as practical, the relative humidity. The first obvious result (Fig. 1.3, bottom) is that the cycle persists, even with a standard diet available throughout the year. Fattening is not dependent on the food available, but, apparently, on an internal response synchronized by the photoperiod (Petter-Rousseaux 1980).

This experiment brought some other unexpected results: while the animals had a fairly homogeneous diet available throughout the year (and this is quite different from the wild conditions), they tended to select foods corresponding to those available during seasonal variations of the natural diet. For instance, in November, at the time of nectar and pollen availability, they neglected animal prey and fed almost specifically on the available sweet carbohydrates. Their attraction for animal protein progressively increased, corresponding to the increase in this food resource that occurs in the wild. In May and June, at

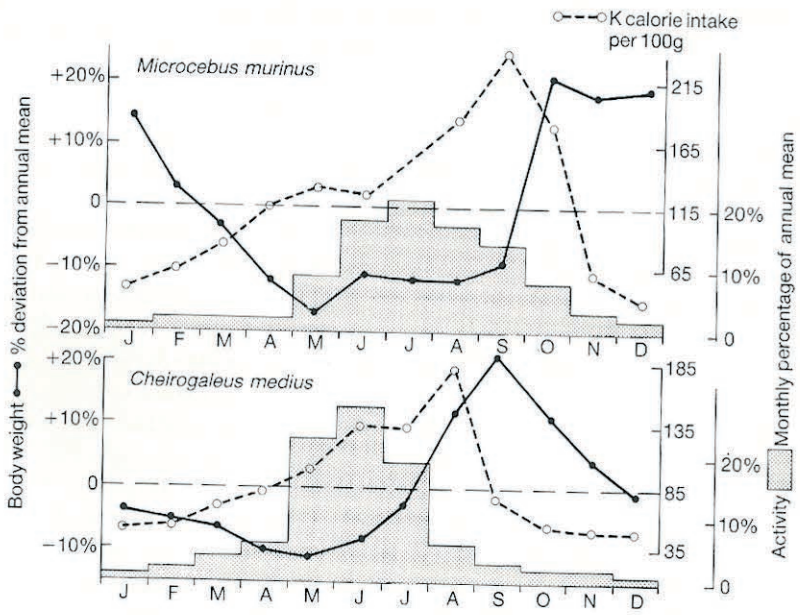


FIG. 1.3. Seasonal variation of body weight (solid line), activity (stippled), and food intake (broken line) of the fat-tailed dwarf lemur, *Cheirogaleus medius*, and the lesser mouse lemur, *Microcebus murinus*, in artificial standard conditions (after Petter-Rousseaux 1980).

the time which normally precedes hibernation, they again tended to select carbohydrates. This resulted in a sharp body-weight increase comparable to that occurring in the wild. This surprising seasonal change in feeding behaviour has been called 'pre-adaptation' (Petter-Rousseaux and Hladik 1980) since the selective choice of the animal seems to anticipate the changes in the food available in the wild.

Can this result be compared to possible changes in human European feeding behaviour, which, in the spring, before cherries ripen on the trees, would develop a tendency towards sweet pulpy fruits? This whimsical extrapolation may not totally be a fantasy. As we will see below, for other primate species, the periodic variation of food resources is the most common case. For a prosimian species subject to the most important variations, the mechanism of periodic adaptation of behavioural physiology was clear enough to be readily apparent. Investigations on other primate species would need more subtle methods to analyse taste specificity and digestive ability.

Coming back to Madagascar, our field study of the lesser mouse lemur (the smallest primate species, weighing 50 to 80 g) brought other results concerning the seasonal aspect of dietary adaptation. This species is not a true 'hibernant' as is the fat-tailed dwarf lemur. During the dry season, the lesser mouse lemur

has a very reduced activity, with torpid periods lasting only for a few days. This animal can also store fat in large quantity in its tail and under the skin, but the increase in body weight is not as important as in the precedent case. It can be seen on Fig. 1.3 (top) (artificial conditions allowing regular control of the body weight) that fattening is more progressive and reaches a maximum about two months after the abrupt body-weight increase preceding hibernation of the fat-tailed dwarf lemur.

The diet of the lesser mouse lemur appears to be fairly similar to that of the fat-tailed dwarf lemur, since the two species feed mainly on the same seasonal stock of 'surplus' food. Fruits form the staple food, but are complemented with a higher proportion of animal matter than in the previous case. Chitin was present in all faecal samples and, at least in one case (when the animal had no time to digest the bait used in the trap), the faeces were exclusively composed of chitin. Direct observation provided evidence of active predatory behaviour directed towards rapid prey such as moths, crickets, and cockroaches. Small vertebrates such as chameleons can also be eaten. It is not surprising to find, in the diet of the lesser mouse lemur, a larger proportion of insects and other small prey than in that of the fat-tailed dwarf lemur, because the two species are able, on the average, to collect similar quantities of animal matter; accordingly, the smallest species obtains, during the same lapse of activity, a relatively higher proportion of protein.

Thus the feeding strategies are slightly different and the lesser mouse lemurs, being active for a longer period at the beginning of the dry season, are able to harvest the rest of this 'surplus food' produced at the wet time, even more thoroughly than the juvenile fat-tailed dwarf lemurs.

Seasonal variations in the diet were equally important in both cases and we also experimentally demonstrated, in the case of the lesser mouse lemur, that variations in food choice, persisting in the absence of variation of the available food, are anticipations of the changes in the composition of the different foodstuffs seasonally available in the wild.

In the two cases, the ability to totally stop or to considerably reduce activity at the time of food scarcity allows the maintenance of large populations in a forest where the total animal biomass would have been seriously limited.

In fact, even in this extreme example, the carrying capacity of a given environment is determined by the cycles of minimum production. According to the diet of the different sympatric species, there is a maximum population level which is never exceeded (Hladik 1981).

To illustrate this remarkably constant phenomenom, I will quote the example of a third prosimian species, the sportive lemur, *Lepilemur mustelinus*, the peculiar name of which is due to its aggressive boxing attitude. One *Lepilemur* species lives in the forest of the west coast of Madagascar where our precedent case study was located, but more accurate measures of the population parameters and seasonal food production were previously recorded in the south of Madagascar (Charles-Dominique and Hladik 1970) and these will be presented.

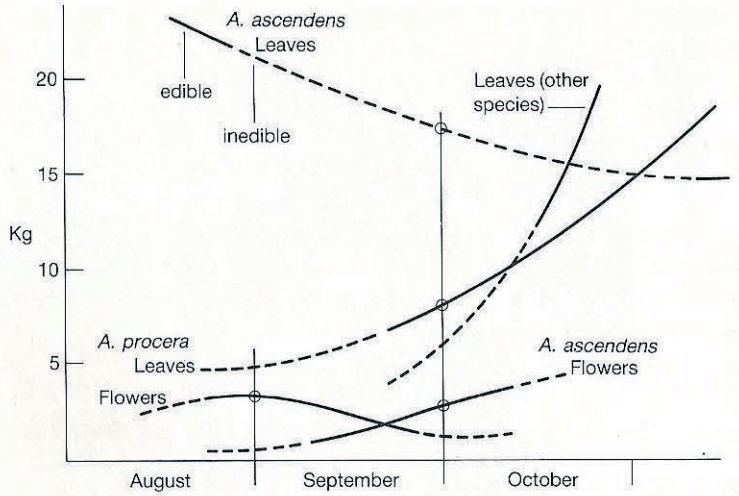


FIG. 1.4. Variation of the food supply available for the sportive lemur, *Lepilemur mustelinus*, in the bush of the south of Madagascar during the period of minimum production. The fresh weight (in kg) of the edible parts of different plant species was calculated in a plot of 2300 m² (after Charles-Dominique and Hladik 1970).

The sportive lemur is one of these highly specialized folivorous prosimians, with a digestive system partly comparable with that of the Lagomorpha (Hladik 1979). Our study took place during the dry season and in a year of exceptional drought (as compared to the records of the ten preceding years). The quantitative analysis of the field conditions is presented in Fig. 1.4, where the production of the different plant species is calculated for an area of 2300 m², that is, the average supplying area of one individual sportive lemur.

At this time, the leaves which normally form the staple food of the sportive lemur are totally shed or inedible (almost dried), and, as usual in this forest type, plants flower before the rainy season. During more than one month, two species (*Alluaudia procera* and *A. ascendens*) provide the flowers which form almost the entire diet of the sportive lemur (see Fig. 1.5).

The population level of the sportive lemur, which has been carefully recorded along transects in different forests of the south and of the west coast of Madagascar, is strictly limited through territorial behaviour regulation, to allow survival during the periods of minimum food production corresponding to our measure (350 sportive lemurs per km²). Population levels of other prosimians feeding on fruits and/or insects are obviously lower than for a folivore, but always limited according to the cycle of food production and its minimum during the period of active feeding.

FIG. 1.5. The sportive lemur, *Lepilemur mustelinus*, foraging at night in the bush of the south of Madagascar. The flowers on top of *Alluaudia procera*, visible on this picture, form the staple during this period of food scarcity, when most plant species have shed their leaves.

LANGURS AND MACAQUES

These simian species live in continental India and in Sri Lanka where it was possible to conduct a field study concerning feeding behaviour in sufficient detail to measure the seasonal effect of the variation of food production occurring in the wild (Hladik 1977a).

In Sri Lanka we found exceptional conditions for field observation: in certain areas, the groups of monkeys which have been in contact with Buddhist pilgrims for centuries tolerate the presence of an observer at a very close distance. Accordingly, it was possible to follow a target animal during the whole day, and to count the number of fruits, leaves, clusters of flowers, etc. that the monkey was ingesting. By this simple method, we have obtained the most accurate records presently available. All the food samples have been collected to measure the average unit weight and to conduct in the laboratory the biochemical analysis. In the field, this study was complemented by a vegetation survey to determine the level of food production in different areas (Hladik and

composition. Two species of leaf monkeys have been compared: the gray langur, *Presbytis entellus*, and the purple-faced langur, *Presbytis senex*. They inhabit a tropical forest of a semi-deciduous type, and share this habitat with the toque monkey, *Macaca sinica*. A nocturnal prosimian species, the slender loris, *Loris tardigradus*, is also present and was subject to local studies, but will not be introduced in this comparative description of simian dietary adaptations.

The diets of the gray langur (Fig. 1.6, bottom) and of the purple-faced langur (Fig. 1.6, top) undergo important variations during the year, as in the precedent case study, depending on the seasonal variation of available food. The cumulative percentages of daily intake of different food categories are presented:

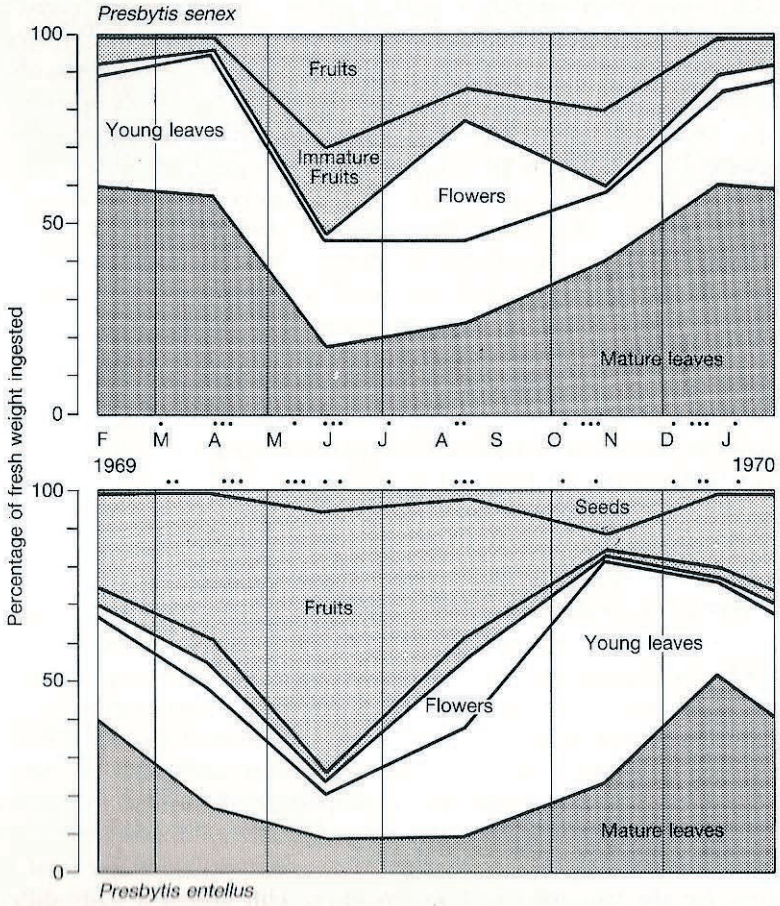


FIG. 1.6. Cumulative percentages of different food categories ingested throughout the

mature leaves; shoots and tender leaves; flowers; immature fruits; mature fruits. The dots along the time axis show the different sampling periods, which have been grouped, to generate sufficient sample size, into two-month successive periods. The resulting graphs indicate the range of the seasonal variations in terms of food intake (total fresh weight).

These graphs illustrate an important methodological point: if we are going to compare the diet of two different species, it is absolutely necessary to sample food intake during the same period, or similar seasons. Consider, for instance, the difference of the quantities of fruits ingested by both species, during the dry season (June–July) and during the wet monsoon season (December). The arbitrary choice of one of these seasons for only one species would totally obscure a comparison, and the species which is in fact the more frugivorous (the gray langur) may appear to eat more leaves than the purple-faced langur.

By contrast, if we compare the food choices of the two species during successive periods of the year, a specific constancy can be clearly observed. At any time of the year, the purple-faced langur (*Presbytis senex*) ingests a larger quantity of leaves, especially of tough mature leaves, and a smaller amount of fruits, especially of mature fruits, than does the gray langur (*Presbytis entellus*). For both species, at the end of the winter monsoon (February–March), the proportion of leaves remains high (95 per cent for the purple-faced langur). The amount of fruits in the diet of both species reaches a maximum during the dry season (June–July): 75 per cent for the gray langur and only 52 per cent for the purple-faced langur. This amount slowly decreases, being replaced by flowers, mainly in August–September, and by new leaves, particularly abundant at the time of the winter monsoon. In December, the total proportion of leaves is around 90 per cent of the diet of the purple-faced langur, but does not exceed 75 per cent of the diet of the gray langur.

The diet of the toque monkey, *Macaca sinica*, is as diversified throughout the seasonal cycle, but with an annual mean of 77 per cent of fruits (including seeds and fleshy pulp) and 4 per cent of animal prey, and can be considered as 'unspecialized' with the meaning defined above (see Fig. 1.7). The proportion of fruits ingested by the toque monkey during the dry season exceeds 95 per cent, while during the winter monsoon rainy season the total proportion of flowers and leaves may reach 45 per cent and approach that of fruits.

According to the percentages of the different food samples ingested at different periods of the year, and after the biochemical analysis of all the food samples, it was possible to calculate the proportion of nutrients in the diet of the different primate species. The resulting graphs (Fig. 1.8 and 1.9) show the variations, in terms of the percentage of the dry weight of the total food ingested, for the two species of leaf-monkey. This allows a quite different interpretation of the intensity of variations which on Fig. 1.6 have the same order of magnitude for both species.

Considering the protein intake (Fig. 1.8), the graph is remarkably flat for the

FIG. 1.7. The toque macaque, *Macaca sinica*, foraging for insects in the undergrowth of the dry forest of Sri Lanka. Protein is the limiting factor for large dispersed groups living in large territories where fruits are abundant.

there are important variations in the diet of the gray langur (broken line), with a minimum at 10 and a maximum at 16 per cent. Similar differences in the intensity of the annual variation can be observed for fats, and to a lesser extent for carbohydrates. The resulting variation in terms of calories and dietary balance would considerably contrast the two primate species.

These differences between primate species have been understood in terms of behavioural physiology (Hladik 1977a), according to other aspects of the field observations. The groups of purple-faced langurs are small (4 to 7 individuals), and they live in a rather limited territory (2 to 7 ha; Rudran 1970) in which they travel for only short distances to feed on the most common food plants. The larger groups of gray langurs (12 to 25 individuals) not only have a wider territorial range (10 to 15 ha), but also are more mobile and active. They have a diet including a large number of plant species, especially the fruit-producing plants such as banian and veera trees (*Ficus bengalensis* and *Drypetes sepiaria*, respectively), for which they will travel long distances and fight against other groups when these food resources are located near the territorial border (Ripley 1970).

The feeding strategy of the purple-faced langur is thus based on a minimum of energy expense which provides a low but regular intake of nutrient. The most variable intake of the gray langur corresponds to a seasonally variable behaviour. The more contrasted annual food cycle of this more active species

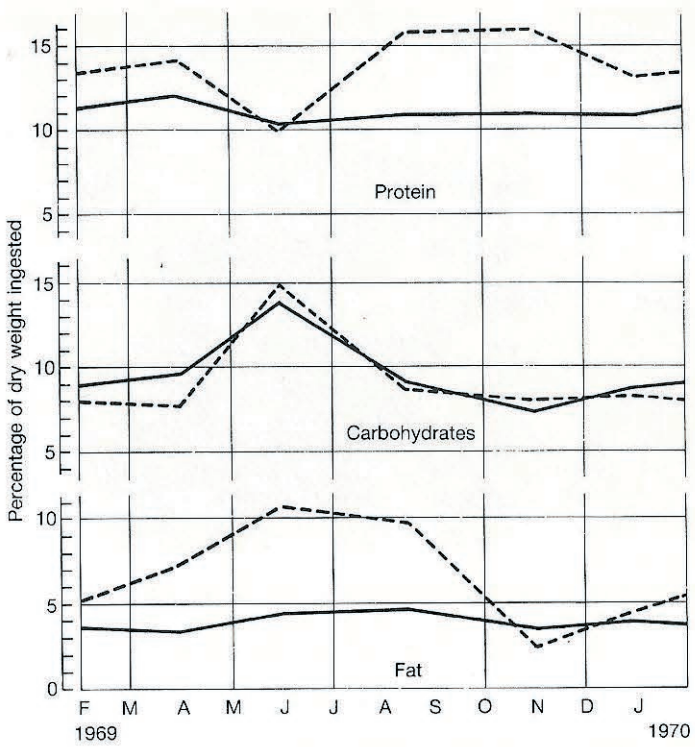


FIG. 1.8. Seasonal variation of nutrients in the diets of the purple-faced langur (solid line) and the gray langur (broken line), in terms of dry weight, during the period of field records presented in Fig. 1.6.

requires an important investment in energy which, in turn, is provided by the more scattered and rich food resources.

The toque monkey is located at a higher energy level in this ecological classification of the feeding strategies, and most of the other primates with 'unspecialized' diets including other macaques, chimpanzees, and *Homo sapiens* are likely to be located at similar levels (Hladik 1981). The groups of toque monkeys include 10 to 40 individuals and range in large territories (30 to 50 ha) very actively (Dittus 1974). An impressive variety of plant species can be used, from which are sometimes selected small amounts of the most nutritious parts. This involves a maximum of energy expenditure with a large seasonal variation (Fig. 1.10). The time engaged in foraging by the juvenile reaches 80 per cent of the active period in November, during the winter monsoon, and is as low as 25 per cent (only 10 per cent for adult males) when the fruits are abundant, in June (Dittus 1977).

As it was suggested in the preface to this volume, these important seasonal variations affecting food intake and behaviour of most primate species are

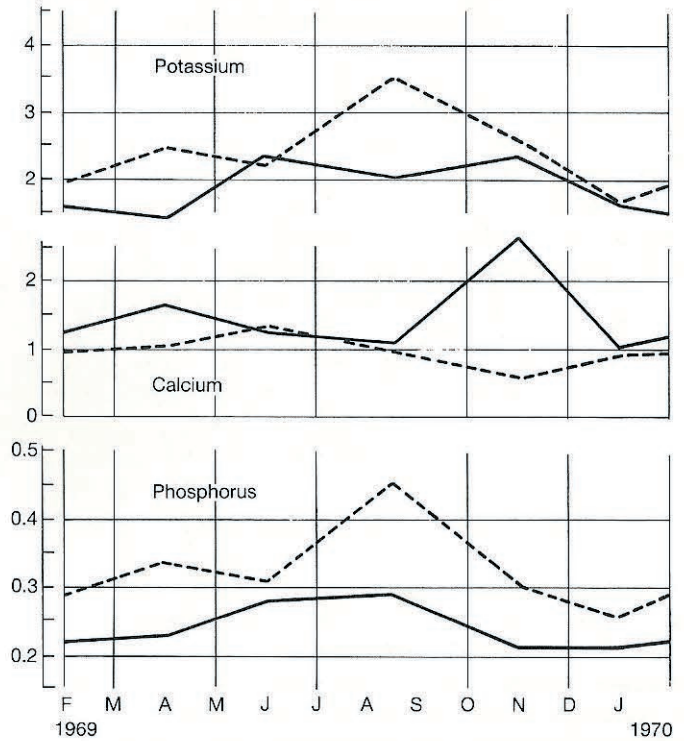


Fig. 1.9. Seasonal variation of minerals in the diets of the purple-faced langur (solid line) and the gray langur (broken line), according to the total dry weight of food ingested during the periods of field records presented in Fig. 1.5.

likely to follow other physiological cycles. Indeed, for most primate species which have been studied in the wild for sufficiently long periods and on large enough population samples, a seasonal birth peak was observed (Rudran 1973). In prosimians, the reproductive cycle is strictly correlated to the food cycle, allowing maximum growth of the juveniles at the time of maximum food production. In simian primates a partly similar ecological mechanism is also apparent, and more investigation would be necessary to determine the physiological basis which allows this type of anticipation of seasonal changes in environmental conditions.

PRIMATES OF THE AFRICAN EQUATORIAL RAIN FOREST

An inventory of the variations of primate feeding behaviour according to food supply would be very unstatisfactory if I did not include a few case studies concerning the equatorial rain forest. Many of the extant primate species inhabit the rain forest, and, in spite of the variations of the area covered by

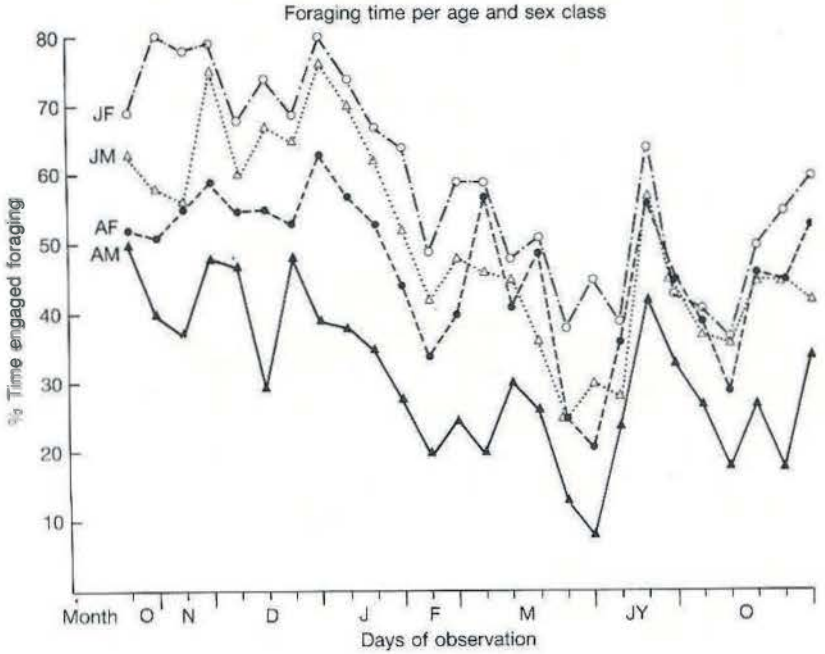


FIG. 1.10. Percentage of the time engaged in foraging at different periods of the year for various age–sex classes of the toque monkey, *Macaca sinica*, in the semi-deciduous forest of Sri Lanka. From bottom to top, the different classes are: adult males (triangles); adult females (black circles); juvenile males (open triangles); juvenile females (open circles). (After Dittus 1977.)

this type of habitat during the last few millions of years, the evolution of several radiations certainly occurred as determined by the environmental conditions.

The extreme complexity of the equatorial forest does not permit the simple and efficient field studies conducted in the dry tropical forest and presented in preceding paragraphs of this paper. For instance, in the last of the successive lists of plants from the Gabon rain forest, the 1233rd species has just been recorded, and several plant specimens are still to be named or determined (Florence and Hladik 1980). During the last ten years, there has been continued activity by different scientists in the forest of Makokou (north-east of Gabon) in order to study the relationships between flora and fauna. Part of the records on plant production and cycles is now available (Hladik 1978), but different field studies are still in progress. Eight species of cercopithecid monkeys inhabit this forest and were the major focus of research by Gautier-Hion and Gautier (1974). My own field studies in Makokou concern the feeding behaviour of the chimpanzee (see below) and some comparative records on gorillas.

Cercopithecidae

The recent work by Gautier-Hion (1980) was carried out with a specific technique which, in spite of the difficulty of observing feeding activity of the monkeys in this forest type, gave sufficient evidence of the cyclic variation in the diet of different species. During several years, containers with 10 per cent formalin were distributed into the villages around Makokou. The local populations in these villages traditionally eat monkey flesh, and the hunters were invited to preserve the stomach content of the monkeys in the containers, accompanied with the head of the animals in order to confirm species identification.

These specimens were analysed after filtering the content through sieves of different mesh size. The fraction of each sieving was sorted out seperately into various food categories with a binocular microscope, dried, and weighed. In a discussion concerning the accuracy of different techniques to measure primate food intake (Hladik 1977a), it was shown that a comparison in terms of dry weight of different food categories is equivalent to the comparative direct records (fresh weight). The juicy parts of some fruits can be omitted with this technique, but after the observations of Gautier-Hion (1980) in the rain forest, most food types were swallowed entirely.

The results of Gautier-Hion (Fig. 1.11) have been grouped according to seasonal changes into five successive periods. Variations of food intake are presented for three different cercopithecid monkeys: the spot-nosed guenon, *Cercopithecus nictitans*; the moustached monkey, *Cercopithecus cephus*; and the crowned guenon, *Cercopithecus pogonias*. Fruits are the staple food for the three species (Fig. 1.11, top), but, while the crowned guenon eats a regular amount (about 80 per cent) throughout the year, there are important variations for the spot-nosed guenon (55 to 90 per cent) and, to a lesser extent, for the moustached monkey. Similar variations appear in leaf intake (Fig. 1.11, middle) which tends to compensate for a lower fruit intake. Concerning the animal matter ingested by the three species (Fig. 1.11, bottom), it seems that seasonal variations are synchronous and may be exclusively due to the variation in invertebrate faunal biomass.

The seasonal variations of food supply are obviously less important in the equatorial rain forest than in dryer types of tropical forests, but remain clearly marked, according to different measures, especially on litter fall (Hladik 1978). The invertebrate production is higher, on the average, than in other forest types (23 kg in dry weight per ha and per year, according to the litter fall measures), but undergoes annual variations, reaching a maximum of availability at the end of the major rainy season and during the minor dry season which follows, from January to March (period I in Fig. 1.11). Fruit production reaches a maximum, at least according to the high number of edible species available at this time (Hladik 1973), at the end of March. This maximum fruit availability clearly appears in the diets of the spot-nosed guenon and the moustached

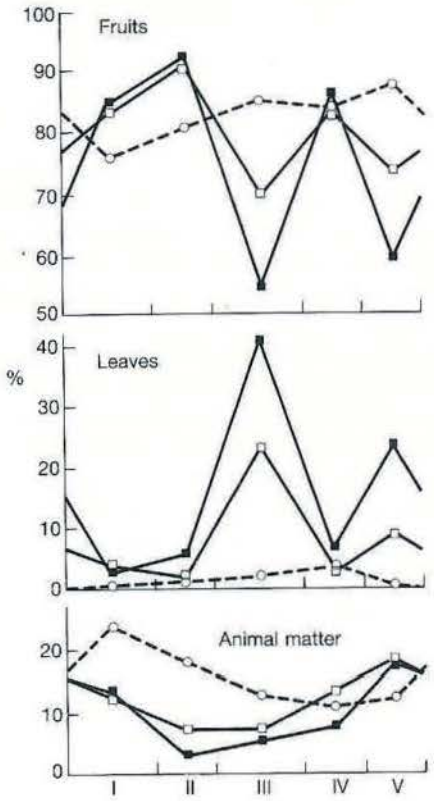


FIG. 1.11. Annual variations in the percentage of dry weight of different food categories found in the stomach contents of three primate species living in the equatorial rain forest: the spot-nosed guenon, *Cercopithecus nictitans* (black squares); the moustached monkey, *Cercopithecus cephus* (open squares); the crowned guenon, *Cercopithecus pogonias* (open circles). (After Gautier-Hion 1980.)

monkey (period II in Fig. 1.11). During the next period (major dry season, from June to mid-August) it seems that fruit scarcity rather than tender foliage abundance is the main factor which determines the folivorous tendency of the two cercopithecid species. In contrast, when tender leaf flush abounds during the major rainy season (periods IV and V, until mid-December) the second peak of folivory in the diet of both species is likely to be due to the opportunity to use this ubiquitous food resource.

Investigations on these primate species of the equatorial rain forest are still in progress, but the careful work of Gautier-Hion (1980) clearly showed the intensity of the dietary variation following an obvious variation of food supply. We do not know to what extent a physiological response to the annual cycle is likely to maintain feeding behaviour, but a certain seasonal pattern was

observed in the reproductive cycles of most tropical mammals, including primates, and is likely to follow the food cycle.

Correlations between primate populations and food availability are more obvious and follow the patterns observed outside of the rain forest (Hladik and Chivers 1978). As it was shown in the preface, there are behavioural and social adaptations which maintain a low population level in order to face the periods of food scarcity. The major food resource for primates (i.e. fruits in the rain forest) is provided not only at irregular intervals throughout the year, but also from year to year. A comparative measure of the same period of fruit production during successive years showed variations reaching 100 per cent (A. Hladik, unpublished data). Accordingly, the different primate species' behaviour might have evolved in order to face this periodical minimum.

Gorillas and chimpanzees

Primatologists concerned with anthropoids are particularly concerned with the relevance of the primate model for human behaviour. Several field studies have been conducted on wild gorillas and chimpanzees, mainly in eastern Africa. The most well known is the Gombe National Park, in Tanzania, where the field work was initiated by Goodall (1963). This area was chosen according to feasibility of field observation in the open parts of the forest.

In the closed equatorial rain forest, it would have been impossible to follow chimp populations in such detail as in the Gombe field studies. Nevertheless, I had an opportunity to work on semi-tamed animals that were reintroduced in the forest of Makokou: if these conditions were very unsatisfying for most behavioural observations, they were extremely useful for allowing an observer to follow the animals at close distance and to use the method previously described for recording, counting, and calculating the weight from the average food sample for every piece of food that the chimpanzees were eating in the wild. During this study I was corresponding with Wrangham who was studying the behaviour of the wild chimpanzees of the Gombe National Park, and we tried to develop similar methods of observation. The comparison which focused on some peculiar aspects of the chimp's feeding behaviour is presented in Hladik (1977b), and a more detailed account by Wrangham (1977) concerns feeding behaviour of the chimpanzees in Gombe National Park.

Figure 1.12 summarizes the results of a one-year field study on this small group of chimpanzees, *Pan troglodytes*, in the Gabon rain forest, carried out in 1971–1972 and complemented by a three-month period of observation during the minor dry season of 1975. The graph follows the variations throughout the year of the cumulative percentages of different food categories ingested by the chimpanzees, in terms of fresh weight. Presentation is in the same order as in Fig. 1.6, the bottom of the graph (dark stipple) showing seasonal variation in the intake of leaves and stems, the middle part of the graph indicating variation in fruit intake. At the top of Fig. 1.12 are separately shown the amount of seeds

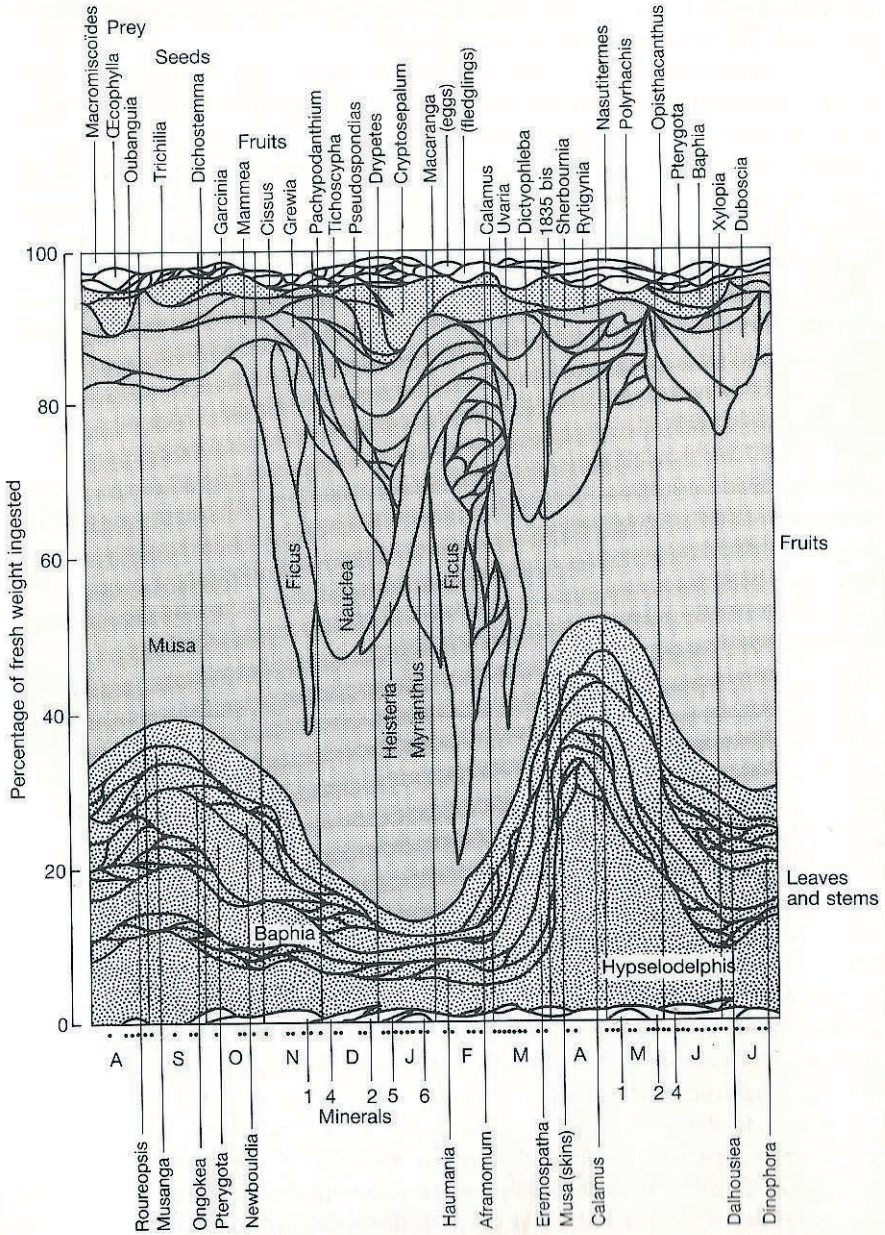


FIG. 1.12. Variations in seasonal food intake of the Chimpanzee, *Pan troglodytes*, in the Gabon rain forest (see comments in text).

(large stipple) and that of invertebrate and small vertebrate prey (white part) ingested throughout the year (see Fig. 1.13).

The sampling periods are indicated by dots along the time axis. During these 12-hour periods of continuous observation it was possible to record and mark the location of the different food samples that were collected and identified during the following days of field work. Accordingly, the annual variation of different food categories presented in Fig. 1.12 has been split into smaller portions which represent each of the different food species, in a list of 210 food items which has been presented elsewhere (Hladik 1973).

This is an illustration of the great variety in the succession of food plants in the rain forest. There are only a few vegetables continuously eaten throughout the year. The stems of a vine, *Hypselodelphis violacea*, is an exceptional and abundant food type that the chimpanzees collect and chew throughout the year. The leaves of a small leguminous tree, *Baphia leptobotrys*, can also be used for long periods but are mainly eaten in the form of shoots and tender leaves which contain the highest proportion of protein ever recorded in primate plant foods (55 per cent of the dry weight; Hladik and Viroben 1974). As for Cercopithecids, the first peak of folivory, during the major dry season, is likely to be due to fruit scarcity rather than to flushing of new foliage.

Concerning fruits, no species is continuously available throughout the year, and the supplement of banana (*Musa sapientum*) available for this group of

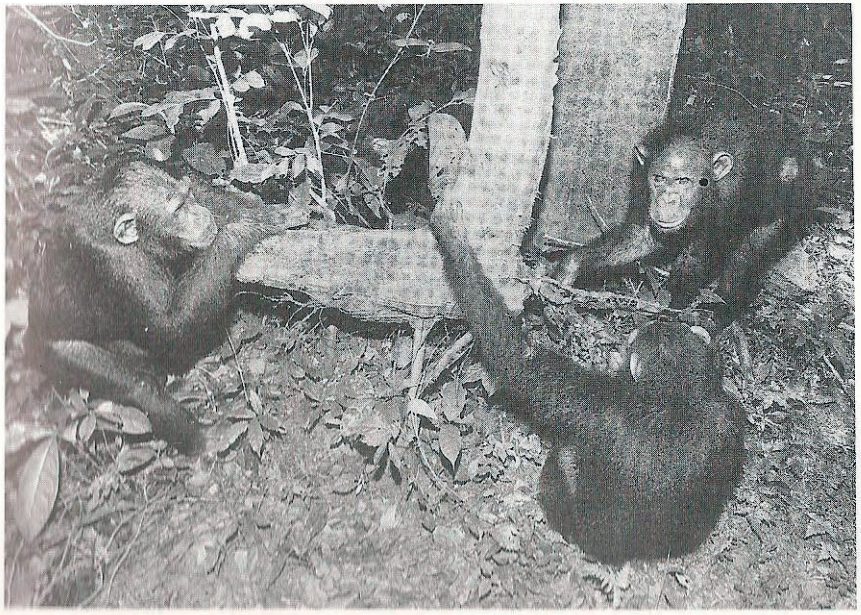


FIG. 1.13. Chimpanzees spend most time foraging for insects: here they are shown extracting ant larvae directly with the hand inside a hollow trunk, in the rain forest, near Makokou, Gabon.

chimpanzees should be split into a greater variety of wild fruits for the other wild groups living in the Gabon rain forest. This was controlled during the observations of 1975 when the animals no longer had supplementary foods and ate 'wild mangoes', *Irvingia gabonensis*, instead of bananas. In Gombe National Park, the wild groups of chimpanzees have also been partly fed with bananas to become familiar to the observers, but, in this area, the number of plant species is smaller than in Gabon and there is a fruit available throughout the year, *Elaeis guineensis*, a palm nut, which can be considered as a staple food.

The seeds of different plant species are eaten, most of them when the fruits are unripe. This is certainly a way to avoid consuming toxic compounds, these being progressively accumulated as the fruits ripen so as to protect seeds against predators.

Invertebrate and small vertebrate prey are mainly composed of ants (in the genera *Macromiscoides* and *Oecophylla*) available throughout the year. For chimpanzees observed in Gombe, termites were more important and more seasonal since they were 'fished' with a stick at the period of dispersal for reproduction. Another difference between Gabon and Gombe was the type of material which accompanied the animal foods: in both cases the chimpanzee is looking for a fibrous vegetable part to chew with the animal prey. In Gabon, bark is peeled out of a tree before the beginning of the meal. In Gombe, only tough leaves are collected and chewed with animal matter. These particular feeding behaviours reflect the social traditions in chimp populations, like other variations throughout the vast geographical range of *Pan troglodytes*, especially concerning the ability of using stones or sticks to break open nuts.

Ingestion of minerals (clay and earth) was observed in Gabon. The small amounts eaten by the chimpanzees are shown at the bottom of Fig. 1.12. Geophagy has been observed in many mammalian species including man, but regular ingestion of earth is observed only in folivorous species. We investigated the nutritional significance of mineral foods in the case of chimpanzee and other primates (Hladik and Gueguen 1974) and found no direct relationship with the mineral content of the rest of the diet: the elements likely to be deficient in the diet were less abundant in the earth samples than in the vegetable food samples. Our hypothesis is that geophagy increases the efficiency of digestion for leaves and other plant parts by preventing tannins to bind with protein. The clay, in particular, can be linked to tannins at the beginning of the digestion and prevent other bindings.

Gorillas are more folivorous than chimpanzees. The field studies by Goodall (1977) and by Fossey and Harcourt (1977) yielded data about menus for gorillas, food composition, and seasonal variation in the amount of different plant species eaten in the wild. These studies were conducted in the montane open vegetation of Rwanda and Zaïre. Gorillas ate mainly leaves and stems of a limited number of species (especially among the genera *Galium*, *Rubia*, *Vernonia*, *Urea*, *Basella*) and some bamboo shoots. The seasonal variations concern the relative proportion of these different plant species, rather than a

radical change in specific foods. Edible fruits are not abundant in these montane areas, but Goodall observed gorillas feeding on *Myrianthus* and *Syzygium*, also found in other rain forest areas.

In the Gabon rain forest, fruits are obviously more abundant in the diet of the gorilla (*Gorilla gorilla*). My personal observations (Hladik 1978) are limited to a few stomach contents of the animals shot by local hunters (who claimed to be attacked by the gorillas) and to a three-month study on a small group of sub-adults introduced into a forested island on the Ivindo River. According to seasonal variation in fruit production, the diet of the gorilla is likely to face more important variations in the equatorial rain forest than in the open vegetation of montane areas (see Fig. 1.14).

In the cases of chimpanzee and gorilla, population density, as far as we can calculate according to the scarce data and from a recent survey by Tutin and Fernandez (1983), is correlated with the minimum level of food production. The biomass of chimpanzee may reach 1 to 1.5 kg per ha, and this is due to the use of leaves and stems in the diet providing a part of dietary protein and partly replacing fruits during the periods of scarcity. Due to its more folivorous diet, the gorilla can be more abundant, but only in terms of biomass and not (due to its large body weight reaching 200 kg) in terms of population density.

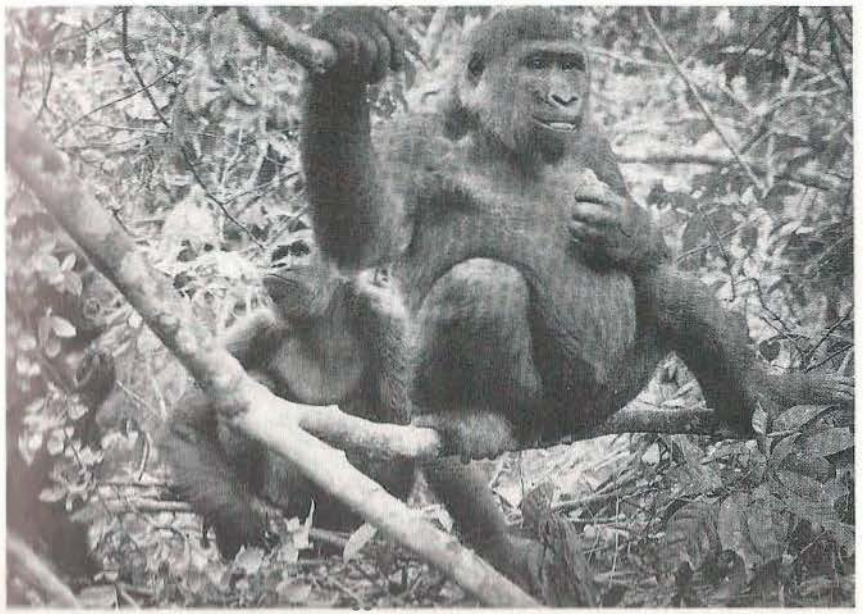


Fig. 1.14. Gorillas in the Gabonese rain forest. Nesting on fruits, leaves, and stems, need a large amount of cellulose, and may re-ingest faeces when food is not abundant or foraging time is limited by bad weather.

DISCUSSION AND CONCLUSION

This ecological background of different species belonging to our own zoological family can be used to determine the possible limits in our primitive conditions and to compare to the present status of certain human populations in a subsistence system.

If man escapes seasonal variations of food supply by different social and/or technological adaptations, for instance, the social system of food sharing of the Aka pygmies described by Bahuchet (1987), the level of food production in the natural environment remains a limiting factor. We calculated the actual biomass of the Aka pygmies, after Bahuchet's data on ranging and 'territories' of different bands in the equatorial rain forest, and found an order of magnitude (around 1 kg per ha) quite similar to that of the wild chimpanzee.

The biomasses of the different primate species are correlated to the levels in food availability which depend on food choices. Summarizing all data available on primate diet, the following relationship has been proposed:
log biomass (in g per ha) = dietary grade, with
grade 1 from pures insectivorous to frugivorous,
grade 2 from frugivorous to folivorous,
grade 3 folivorous,
and all intermediate results corresponding to intermediate cases in the dietary adaptation (Hladik 1981). The introduction of a logarithmic notation tends to reduce small differences and allows comparison of different tropical forests. The variation in the biomass is large enough to have a similar order of magnitude in these different environments.

Accordingly, it was not surprising to find similar orders of magnitude in the biomasses of wild primate populations and in the human population using rain forest resources and belonging to the same 'dietary grade'.

Seasonal and year to year variations have the same result in both cases. In the rain forest of Central Africa (which belong to the same forest block as Gabon and Zaïre), these variations, or ecological constraints (Bahuchet 1978), are important, especially for fruit availability and edible insects (caterpillars and termites).

Coming back to our primate model, variations in food supply may have an important effect on different physiological mechanisms, as was clearly observed for prosimians and simian primates living in dry tropical climates. There is no reason to believe that some aspects of these seasonal variations of the physiological parameters could be totally absent in the rain forest, since there are also variations in composition and abundance of the foods available. The body weight of the sub-adult chimpanzees observed in Gabon (see preface) varied according to a periodical pattern, being stable during the major dry season and with a sudden increase at the period of maximum fruit production.

These periodical variations, in the short term (annual) and with an unpredictable year-to-year pattern, have been avoided by the technical and socio-

logical organization of the human society. They are still perceived in different groups using a part of the natural resources such as the Ntomba in Zaïre (Pagezy 1987) in spite of the important use of crop plants. Can these variations be totally ignored in our industrial societies? They are a part of the physiological mechanisms of the primates, and a total loss of this adaptation to cope with uncertainty in food supply may not be a progress in human evolution.

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